



Recovery of floristic diversity, composition and structure of regrowth forests on fallow lands: implications for conservation and restoration of degraded forest lands in Laos

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Abstract

In Laos, there are extensive shifting cultivation areas and regrowth forests spontaneously established on fallow lands. The aims of the study were to conduct a comparative study of old-growth and regrowth forests in terms of structure, woody species diversity and composition as well as to investigate the potential role of regrowth forests in the conservation and restoration of degraded forest lands in Laos and the tropics in general. Systematic plot sampling was used to survey the floristic diversity, species composition and structure of old-growth and regrowth forests. Concentric circular plots with an area of 200 m² and 500 m² were laid on line transects. A total of 24 plots were sampled from two sites. In comparison to regrowth forests, old-growth forests had higher structural heterogeneity because of higher canopy height variations, vertical stratification, and tree sizes and their variations. Species richness and diversity indices values were similar, but abundance and species composition were significantly different between old-growth and regrowth forests. It appears that species richness recovers first followed by forest structure and species composition. Regrowth forests are important for in situ conservation of tropical biodiversity and they can also serve as a conduit for the restoration of degraded lands and forests. Regrowth forests provide habitats, serve as buffer zones around the fragmented old-growth forests, function as source of propagules, and enhance landscape connectivity. Utilization of regrowth forests for restoration purposes is comparatively inexpensive. Regrowth forests should be given the due considerations in the national forest conservation and restoration policy of Laos.

Keywords Biodiversity · Old-growth forests · Regrowth forests · Shifting cultivation · Conservation · Restoration

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Introduction

Shifting cultivation, which is a dominant agricultural system covering about 280 million hectares and practiced by 300–500 million people around the world, remains an important driver of change in the tropical forests (Liao et al. 2015; Heinimann et al. 2017). In many parts of South East Asia, shifting cultivation or swidden has been generally carried out for decades for rice and secondary crop production (Metzger 2003; Fukushima et al. 2008; Teegalapalli and Datta 2016). In the forest-agriculture transition zones, pioneer swidden typically begins by clearing and burning of vegetation to pave the way for cultivation. Subsequently, regrowth forests can spontaneously regrow along those margins during the cyclic periods (fallow) when cultivation is suspended to allow for natural recovery of soil nutrients. In this article the term regrowth forest is used instead of secondary forest and it is defined as native forests containing a substantial proportion of trees in a younger growth phase, which are vigorously growing and may contain scattered individuals of mature trees [modified from AFS (2007)].

Estimates of the global area of land currently abandoned after swidden is difficult to ascertain, as the reported extent of areas under the agricultural practice vary considerably in the literature. The reported figures vary by reporting source and means of estimation. However, an FAO report (Lanly 1982) estimated the total affected area at 410 million hectares (Mha) by 1980. Current studies based on more reliable multi-temporal Landsat assessments (which delimit forest extent and change) put the global figure at 280 Mha (Heinimann et al. 2017), indicating a 30% decline from the 1980 total.

In Lao People's Democratic Republic (Laos) stands where the slash and burn agriculture is practiced is known by the Lao name, *hai*. The aggregate area affected by swidden agriculture had expanded to about 6.5 Mha in 1999, but has since declined to about 4 Mha (Gansberghe 2005; Liao et al. 2015; Heinimann et al. 2017). Slash and burn agriculture is practiced by about 17% of the Lao population and occurs on 29% of the land area of the country (Messerli et al. 2009). Shifting cultivation is considered as one of the main reasons for forest loss as well as forest and land degradation in Laos (Phompila et al. 2017). In spite of ongoing attempts to eradicate the age-old farming practice, the slash and burn agriculture is still practiced over extensive areas of the country. The limited availability of alternative livelihood sources in rural parts of Laos is one of the main reasons for the perpetuation of the slash and burn agricultural practice (Heinimann et al. 2017).

A number of recent studies have confirmed a rampant trend in swidden abandonments for alternative land uses and livelihood across South East Asia. The common pattern is that the former *hai* land, once abandoned, is quickly reverted to other intensive land uses such as tree plantations. However, in other cases where the land remains free of intensive land-uses, what often follows is the natural process of ecological succession leading to the re-establishment of regrowth forest. In the lower Mekong basin, such regrowth forests constitute the largest share of all forest types, with up to 80% of this forest type located in Laos and Cambodia (Sovu et al. 2009). In Laos, regrowth forests are important sources of local livelihoods and provide ecosystem services (Heinimann et al. 2017; Phompila et al. 2017).

It has been well-documented that such abandoned fields are initially colonized by abundant early-successional and some shade-tolerant species, whose community dynamics is mainly influenced by recruitment, competition, mortality, and species turnover (van Breugel 2007). According to the classical relay floristics understanding, following the removal of disturbance, pioneer and later stage communities will progressively occupy fallow sites, each giving way to successor until the emergence of a climax community.

Barring human intervention, the initial floristic composition is largely a function of species dispersal by natural vectors, resprouting from stumps and root suckers and regeneration from soil seed bank (Egler 1954; Wheeler and Cullen 1997; Kammesheidt 1999; Norman et al. 2006; Vieira and Proctor 2007).

With the recent global trend of swidden abandonment for other means of livelihoods, such regrowth forests provide an excellent opportunity for the examination of long-term successional changes in vegetation (Teegalapalli and Datta 2016). In the last two decades, there has been a growing research interest to examine the pattern of species diversity and biomass recovery in regrowth forests on former swidden land in South East Asia (Widiyatno et al. 2017). This understanding of ecological succession forms the bases of the passive and active reclamation approaches in the now burgeoning science and practice of ecological restoration (SER 2004; Walker and del Moral 2008; Jacobs et al. 2015). Following this development, the broader ecological and conservation literature has started giving more attention to the potential of regrowth forests in facilitating landscape restoration (Chazdon et al. 2009; Chazdon 2014). However, because of the various factors (biotic and abiotic) and their complex interactions that influence forest succession, the rate and trajectory of vegetation change on former fallow lands is still not well understood (Turner and Dale 1998; Mwampamba and Schwartz 2011; Maza-villalobos et al. 2017).

The aims of this study were to: (1) conduct a comparative study of old-growth and regrowth forests which are established via autochthonous colonization on fallow lands in terms of structure, woody species diversity and composition; (2) investigate the potential role of regrowth forests spontaneously established on fallow lands in the conservation and restoration of degraded forest lands in Laos.

As shifting cultivation and the subsequent regrowth forests are widespread throughout the world, the results of this study can be applicable for the conservation of biodiversity and restoration of degraded forest lands in different parts of the tropics.

Materials and methods

Study sites

The study sites are located in Napo (18°16'41"–18°16'21"N and 102°11'13"–102°10'43"E) and Dong Na Tard (16°37'07"–16°37'02"N and 104°51'07"–104°50'41"E) which are situated in the Vientiane prefecture and Savannakhet province, respectively (Fig. 1). The elevation of the study site in Napo ranges 234–300 and in Dong Na Tard it ranges 163–174 m.a.s.l. The climate in Laos is influenced by the Asian monsoon with distinct rainy (May to September) and dry (October to April) seasons and the average rainfall is ca. 1780 and 1610 mm/year at Napo and Dong Na Tard, respectively (Suzuki et al. 2008; McNamara et al. 2012). The temperature at Napo and Dong Na Tard is by and large similar. At both sites, the mean annual temperature is 27 °C, while the mean monthly minimum and maximum temperature is 23 °C and 30 °C, respectively (NOAA 2019).

The natural forest at Dong Na Tard which receives relatively less precipitation, and which has a higher occurrence of dipterocarp species is classified as lower mixed deciduous forest (FAO 2010), while the natural forests at Napo lie between an upper mixed deciduous forest and an upper dry evergreen forest (Sovu et al. 2009). Clusters of bamboo are found in both forests. The regrowth forests at Napo and Dong Na Tard are 10 and 15 years old, respectively.

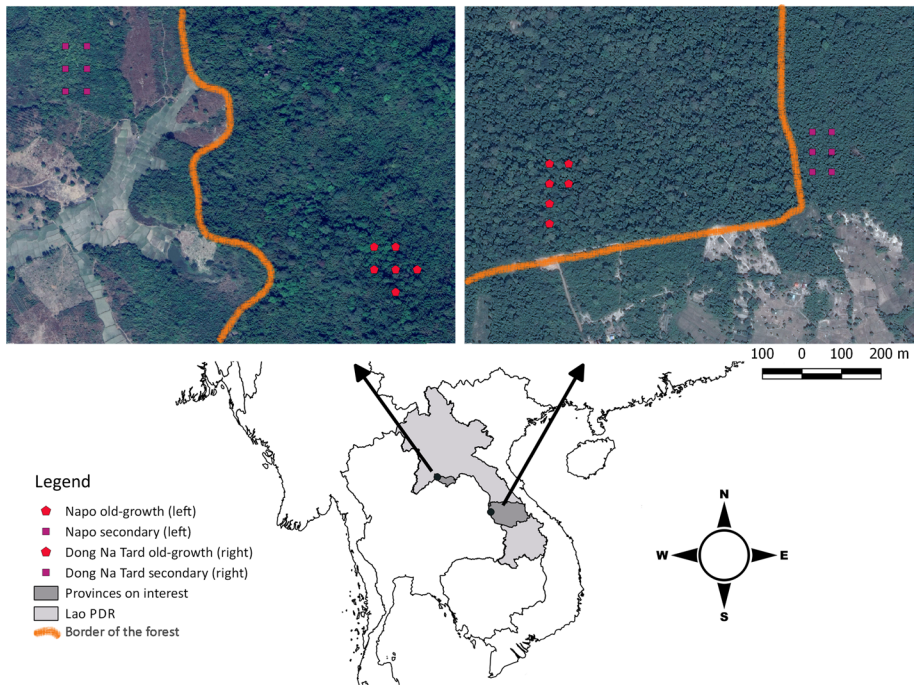


Fig. 1 Map showing the locations of the study sites at Napo and Dong Na Tard, Laos

Forest inventory design

Systematic plot sampling was used to survey the structure, floristic diversity, and species composition of the old-growth and regrowth forests at Napo and Dong Na Tard. The initial plot in all stands was randomly selected and the coordinates of the centre of the plot were recorded using a GPS. Two concentric circular plots with a radius of 7.98 m and 12.62 m, which constituted an area of 200 m² and 500 m², respectively were laid on two line transects (except in Napo old-growth forest where we had three line transects). The distance between the sample plots on a line transect and between line transects was 50 m. Six sample plots were laid on the line transects in each forest type at both study sites, i.e. a total of 24 plots were sampled. The total sampled area was 1.2 ha.

Forest structure

The sample plot for measurement of structural attributes contained two concentric circular subplots (200 m² and 500 m²). In the small plots all individual trees between 5 and 20 cm breast height diameter (dbh) were measured, whereas in the bigger plots, the inventory was restricted to trees greater than 20 cm in diameter.

For the purposes of biomass estimation, diameter at breast height (dbh) was measured at 1.3 m height for all trees within the plots using a tallmeter (diameter tape). Trees with a dbh less than 5 cm were not measured. For trees with multiple stems, all stems were

measured, and square root of the sum of all squared stems was calculated to represent the dbh of trees.

Heights of every third tree in a plot were measured using a hypsometer. Additional trees (dbh > 50 cm) were included in the sampling of heights to compensate for their low frequency. The tallest stem was chosen to represent the height of a tree with multiple stems. A generic equation for Continental Asia by (1) Feldpausch et al. (2011) was the best fit to explain the observed heights and was used to estimate heights for all trees. Dead trees were skipped in height measurements; the next living tree was measured instead.

$$\log(H) = 1.2156 + 0.5782 \times \log(DBH) \quad (1)$$

where H is in meters and DBH in centimetres.

Each tree was also assigned to a relative canopy dominance class based on the position of the tree's crown in relation to the crowns of surrounding trees. Trees that were subject to practically no competition were assigned to dominance class one. Trees sharing crowns in the main canopy layer were assigned to class two and trees in the understory were assigned to class three. Tree diameter or height were not used to determine dominance, but class estimates are based on ocular estimates of canopy dominance.

Floristic diversity and composition

For surveying floristic diversity and composition, the circular plot with a radius of 7.98 m (an area of 200 m²) was subdivided into four quadrants. Within each quadrant we surveyed woody species, climbers and epiphytes and the herbaceous layer. In addition, a meeting was held with village elders to discuss research site history as well as the flora and fauna of the study area.

Woody species

In each plot, woody species were identified and counted with the help of parataxonomists and botanical keys. Woody plants were grouped by size classes as: seedlings (0.05 < height < 1.3 m), saplings (height ≥ 1.3 m and dbh < 2.5 cm) and mature trees. Germinants (height ≤ 0.05 m) were neither identified nor counted. The vegetation survey was carried out quadrant by quadrant in a clockwise direction.

Climbers and epiphytes

The dominant climber and epiphytes species were identified in all sample plots. The species were identified with the help of local parataxonomists and botanical keys.

Herbaceous plants

In each sample plot, five 1 m² quadrats were randomly placed for identification and estimation of the ground cover percentage of herbaceous species. The four 1 m² quadrats were placed randomly in each of the four quadrants of the circular plot. The fifth 1 m² quadrat was randomly placed near the centre of the circular plot. To improve the estimation of the ground cover percentage the 1 m² quadrats were divided into four square quadrants and the estimation was done quadrant by quadrant. Moreover, pictures of the 1 m² quadrats were

taken for species identification and estimation of the ground cover percentage. The average of the five values was used to estimate the ground cover percentage of each sample plot.

Data analysis

Plot-level woody biomass was calculated as the sum of all living trees on the plot using a general equation for moist tropical forests (2) by Brown (1997) and modified by Pearson et al. (2005). Site-specific biomass was calculated as the simple arithmetic average of generalized plot results. The carbon fraction was assumed to be 47% of the biomass, as outlined by IPCC (Aalde et al. 2006).

$$\text{Biomass} = e^{[-2.289 + 2.649 \times \ln(\text{DBH}) - 0.021 \times \ln(\text{DBH})^2]} \quad (2)$$

where Biomass is in kilograms and DBH in centimetres.

Canopy closure was estimated using hemispherical photographs taken with a Sigma 8 mm fish-eye lens attached to a Canon EOS 700D camera. Four digital photographs were taken in the centre of each plot and they were later analysed using the DHPT 1.0 software. DHPT 1.0 applies a hue-enhancing method before automatically calculating the threshold that will separate canopy from sky pixels (Loffredo et al. 2016). Table 1 shows the average canopy closure for each forest.

In addition to species richness and abundance, Shannon and Simpson diversity indices were used to measure woody species diversity in old-growth and regrowth forests. Shannon evenness was used to separately calculate the species evenness. The Bray–Curtis index was used to measure the similarity in woody species composition of the old-growth and regrowth forests. The R version 3.4.2 was used to calculate diversity and similarity indices (R Core Team 2017).

One-way fixed effects ANOVA (analysis of variance) was used to detect differences in the means of species richness, abundance, Shannon, Simpson, and evenness between old-growth and regrowth forests for each study site. Significantly different means were compared by Tukey multiple comparison tests. Similarly, one-way ANOVA and Tukey's HSD test were used to detect variations in stand structure attributes. The mean square of the within group variance was used as the denominator of the F-ratio. The Shapiro–Wilk test was used to check normality of the data distribution.

Table 1 Diameter at breast height, height, basal area, biomass and canopy closure of old-growth and regrowth forests at Napo and Dong Na Tard. Breast height diameter, height, basal area, and above ground biomass (AGB) values are followed by standard of deviation

Stand	Mean dbh (cm)	Mean height (m)	Mean BA (m ² ha ⁻¹)	AG biomass (Mg ha ⁻¹) ^a	Canopy closure (%)
Napo OGF	21.96 ± 20.42	14.79 ± 12.55	25.16 ± 6.18	290.13 ± 83.02	92.61
Napo RGF	7.27 ± 2.23	5.77 ± 1.37	2.19 ± 1.35	10.35 ± 7.12	90.91
DNT OGF	17.59 ± 16.41	12.10 ± 10.08	23.39 ± 10.22	243.13 ± 144.10	92.11
DNT RGF	10.16 ± 5.54	7.54 ± 3.40	8.64 ± 2.97	53.15 ± 23.90	84.88

OGF old growth forest; RGF regrowth forest; DNT Dong Na Tard

^aAG biomass was estimated using the equation by Pearson et al. (2005)

A non-metric multidimensional scaling (NMDS) ordination based on Sørensen's quantitative similarity index (as a distance measure) was used to investigate the similarity/dissimilarity of the old-growth and regrowth forests in terms of woody species composition. The NMDS was carried out using PC-ORD for Windows software (version 6.15). A random starting configuration with stability criterion of 10–5 was used and 200 iterations were conducted, which resulted in a two-dimensional solution. A Monte Carlo test was conducted to evaluate whether NMDS extracted stronger axes than expected by chance (McCune and Grace 2002). For the Monte Carlo test, 50 randomized runs were carried out and the probability that a similar final stress could have been obtained by chance was very low ($P < 0.05$).

Multi-response permutation procedures (MRPP) was used to test differences in species composition between the plant community groups and to test within-group homogeneity. The Sørensen distance measure was used in the MRPP analysis.

An indicator species analysis was conducted to identify the indicator species for the plant community groups in the old-growth and regrowth forests. In this study, plant species which had the highest indicator values and $P < 0.05$ were designated as indicator species. In the indicator species analysis, the Monte Carlo test of significance of observed maximum indicator value for each species was based on 4999 randomizations.

Rare species were determined for both the old-growth and regrowth forests at Napo and Dong Na Tard. In this study, rare species were defined as species represented by a single individual (singleton) (Magurran 2004).

Results

Stand structure

The height and dbh as well as the associated stand attributes of basal area and above ground biomass were considerably smaller in the regrowth forests than in the old-growth forests. The regrowth forests have dbh and height of 33–58% and 39–62% of the corresponding old-growth forests, respectively. In addition, there was a higher variation in height and dbh values of old-growth forests, which is indicated by the higher standard of deviation (Table 1, Fig. 2).

Both old-growth forests (OGFs) reported a similar basal area per hectare, but Napo's OGF had a bigger share of that basal area allocated in larger trees. Differences between regrowth forests are larger due to the presence of some remnant trees in Dong Na Tard secondary forest (Table 1). The scattered presence of these remnant trees also influenced canopy closure in Dong Na Tard's regrowth forest which is significantly lower ($P < 0.005$) than other forest stands in this study.

For above ground biomass, variation between plots was larger in Dong Na Tard's plots than in Napo's plots, both for old-growth forest and regrowth forests (Fig. 2). Nonetheless, a comparison of means, showed no significant difference within sites or between sites for old-growth forest plots at a 95% confidence interval; the same applies for regrowth forest within sites. However, AGB values for regrowth forest were significantly different between sites.

Biomass in old-growth forests was concentrated in large dominant trees. About 80 and 60% of the AGB was contributed by the dominant trees in Napo and Dong Na Tard, respectively (Fig. 3). Dominant trees in Napo were 35–45 m in height while

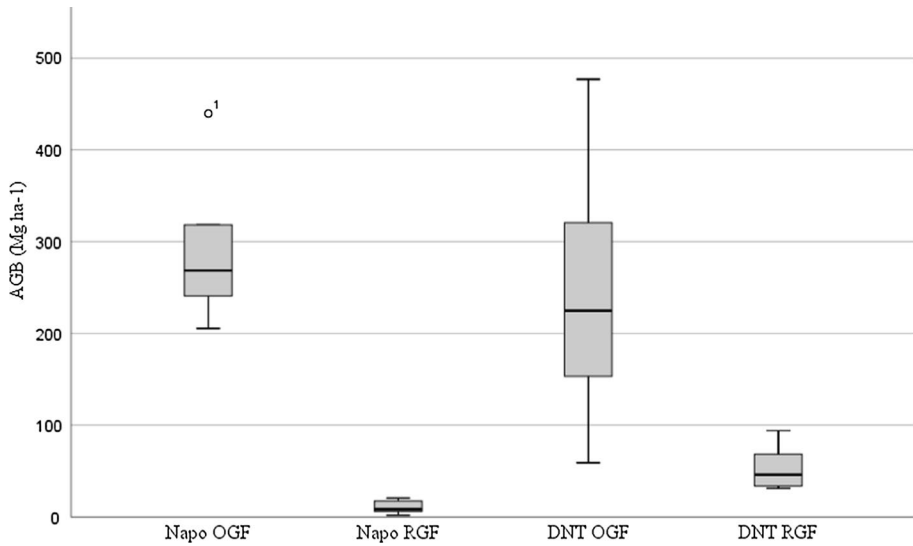


Fig. 2 Above ground biomass for the old-growth and regrowth forests in Napo and Dong Na Tard

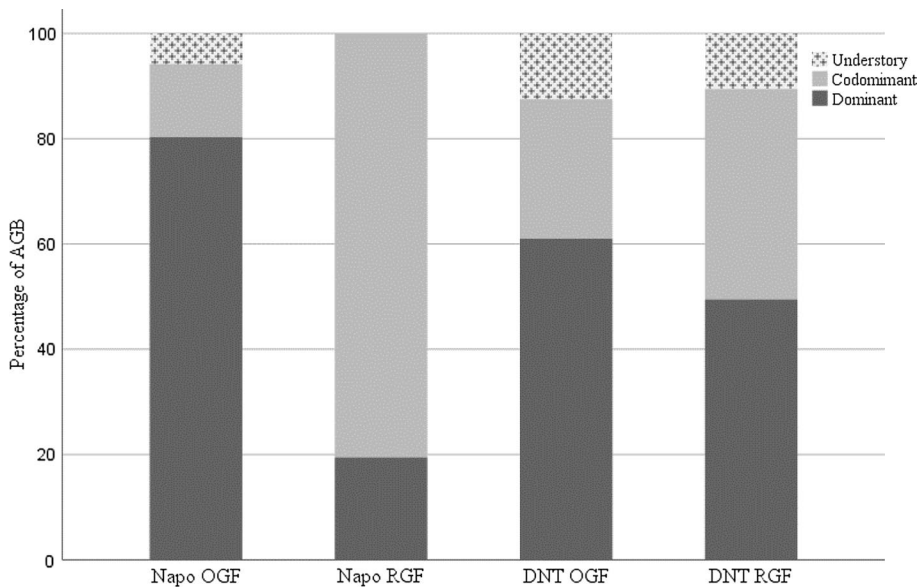


Fig. 3 Distribution of above ground biomass according to dominance classes for the old-growth and regrowth forests in Napo and Dong Na Tard

codominant trees reached 25–35 m; Dong Na Tard had less emergent trees and the codominant canopy was as tall as in Napo. On the other hand, the regrowth forests had a more homogenous canopy and contained fewer dominant emergent trees and as result the contribution of the dominant trees to AGB was lower and the codominant trees was

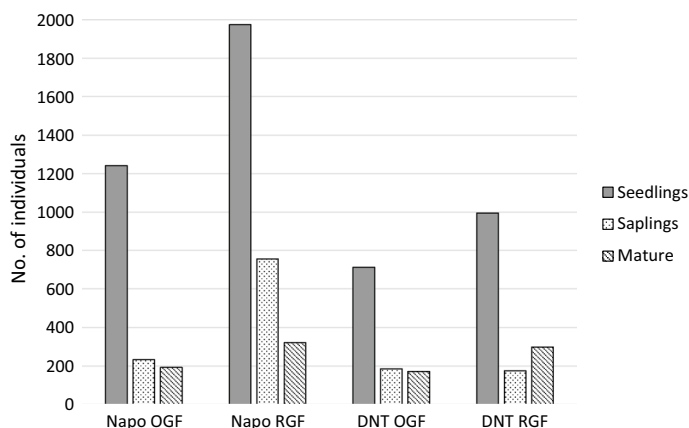


Fig. 4 Seedlings, saplings and mature woody species in old-growth and regrowth forests in Napo and Dong Na Tard

Table 2 Species richness, abundance, diversity indices and evenness for the old-growth and regrowth forests in Napo

Stand	Species no.	Abundance	Shannon index	Simpson index	Evenness
Napo OGF	34.7 (1.71) ^a	275 (11.83) ^a	1.298 (0.04) ^a	0.08 (0.01) ^a	0.84 (0.02) ^a
Napo RGF	38.0 (2.76) ^a	515 (47.45) ^b	1.353 (0.06) ^a	0.07 (0.01) ^a	0.86 (0.02) ^a
<i>t</i> value	−0.861	−4.459	−0.588	0.329	−0.399
<i>P</i> value	0.428	0.007	0.582	0.756	0.706

The number in parenthesis indicates standard error of the mean. Means sharing the same letter (a or b) are not significantly different at $P < 0.05$

higher than old-growth forests. In Napo regrowth forests had a more even canopy dominated by 8 to 12 m tall trees, while in Dong Na Tard regrowth forests and dispersed remnant trees reached between 15 and 20 m in height. In addition, the contribution of the understory to the AGB of regrowth forests was particularly low in Napo forests.

The size class distribution of the regrowth forests showed a reverse-J shaped pattern with a sharp drop from the younger to the mature class (Fig. 4). This pattern is also manifested by the considerably higher combined number of seedlings and saplings in the regrowth forests than in the old-growth forests, i.e. 1.85 and 1.3 times higher in Napo and Dong Na Tard, respectively.

Woody species diversity

Diversity indices and evenness values were by and large similar in the regrowth and old-growth forests at both sites. However, the woody species richness was similar in

Table 3 Species richness, abundance, diversity indices, and evenness for the old-growth and regrowth forests in Dong Na Tard

Stand	Species no.	Abundance	Shannon index	Simpson index	Evenness
DNT OGF	28.33 (1.48) ^a	178 (27.1) ^a	1.09 (0.04) ^a	0.14 (0.02) ^a	0.76 (0.01) ^a
DNT RGF	35.17 (2.06) ^b	249 (19.8) ^b	1.18 (0.03) ^a	0.11 (0.01) ^a	0.77 (0.03) ^a
<i>t</i> value	−2.68	−3.079	−1.728	1.465	−0.42
<i>P</i> value	0.044	0.027	0.145	0.203	0.692

The number in parenthesis indicates standard error of the mean. Means sharing the same letter (a or b) are not significantly different at $P < 0.05$

Napo, but differed between the forests in Dong Na Tard. On the other hand, woody species abundance was significantly higher in regrowth forests, particularly in Napo which was 1.9 times higher than in the old-growth forest (Tables 2, 3).

Floristic composition

There was a significant difference in woody species composition between the old-growth and regrowth forests both in Napo and Dong Na Tard (Fig. 5a,b, Table 4). This difference seems to be even more pronounced in Napo (Table 4). There was a moderate heterogeneity in woody species composition within the old-growth and regrowth forests as indicated by the positive *A* values in the MRPP analysis (Table 4). In Table 4, *T* describes the separation between the old-growth and regrowth forest. The more negative *T* is, the stronger the separation. *A* indicates within group homogeneity. If $A = 1$ all items within groups are identical. $A = 0$ when observed heterogeneity equals the expected. $A < 0$ when there is significant difference within groups.

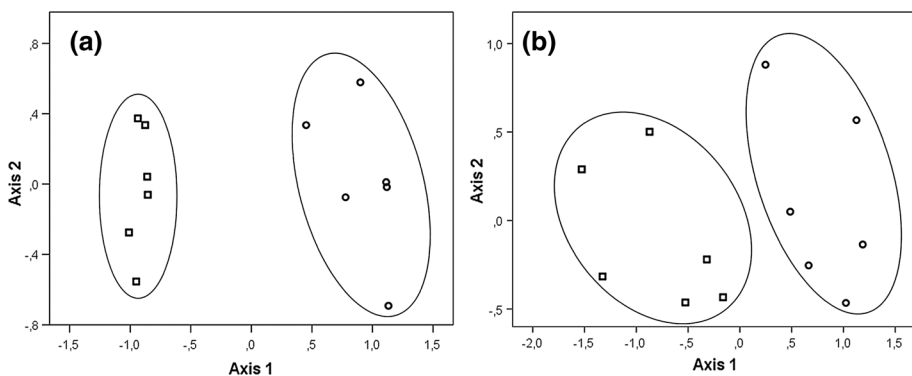


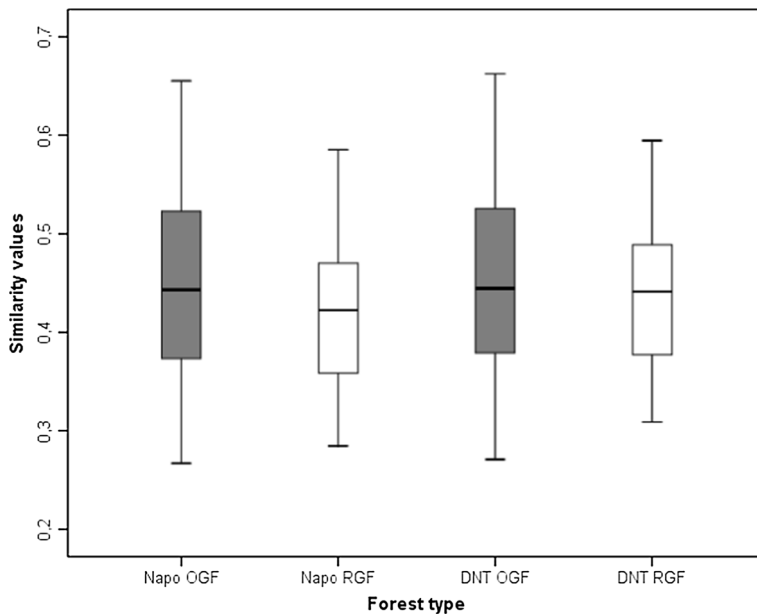
Fig. 5 a, b Non-metric multidimensional scaling (NMDS) ordination of the old-growth and regrowth forests in Napo (a) and Dong Na Tard (b). The circle represents the old-growth forests while square represents the regrowth forests

Table 4 MRPP analysis for the old-growth and regrowth forest woody species communities in Napo and Dong Na Tard

	T	P	A
Napo	−6.18	< 0.001	0.23
Dong Na Tard	−3.01	< 0.05	0.07

T describes the separation between the groups

A describes within group homogeneity, compared to the random expectation

**Fig. 6** Within group similarity values of old-growth and regrowth forest sample plots in Napo and Dong Na Tard

Within group similarity between sample plots

The standard deviation of the Bray–Curtis similarity index of the sample plots in the old-growth and regrowth forests at Napo was 0.1157 and 0.0925, respectively. Likewise, the standard deviation values for the old-growth and regrowth forests at Dong Na Tard was 0.1147 and 0.0892, respectively. The higher range of similarity values of the old-growth forests compared to the regrowth forests is also indicated by Fig. 6. This implies that the variation in woody species composition between the regrowth forest plots is less than those in the old-growth forest.

Indicator species analysis

The set of indicator species for the old-growth and regrowth forests were different at Napo and Dong Na Tard (Table 5a, b).

Table 5 Indicator species for the old-growth and regrowth forest in Napo (a) and Dong Na Tard (b)

Old-growth forest			Regrowth forest		
Species	IV value	P value	Species	IV value	P value
(a)					
<i>Aglaia gagnepainiana</i>	100	0.0018	<i>Lepisanthes rubiginosa</i>	100	0.0018
<i>Hopea ferrea</i> [EN]	100	0.0018	<i>Saraca declinata</i>	95	0.0048
<i>Mirabilis jalapa</i>	100	0.0018	<i>Melanorrhoea laccifera</i>	71	0.0048
(b)					
<i>Parashorea stellata</i> [VU]	97	0.0022	<i>Polyalthia suberosa</i>	87	0.0022
<i>Lasianthus hoaensis</i>	83	0.0132	<i>Diospyros filipendula</i>	87	0.0080
<i>Xylopia vielana</i>	75	0.0368	<i>Anisoptera costata</i> [EN]	86	0.0330

The indicator values (IV) are tested for statistical significance using the Monte Carlo technique

VU vulnerable, EN endangered

Table 6 The list of threatened species in the old-growth and regrowth forests in Napo and Dong Na Tard

IUCN classification	Scientific names	OGF	RGF
Napo forest			
NT	<i>Dalbergia cultrata</i>		x
NT	<i>Dialium cochinchinense</i>	x	
VU	<i>Cinnamomum litsaefolium</i>	x	x
VU	<i>Dipterocarpus alatus</i>	x	
VU	<i>Shorea roxburghii</i>	x	
VU	<i>swietenia macrophylla</i>	x	x
EN	<i>Dalbergia oliveri</i>	x	
EN	<i>Hopea ferrea</i>	x	
EN	<i>Shorea hypochra</i>	x	
Dong Na Tard forest			
NT	<i>Dialium cochinchinense</i>	x	x
VU	<i>Diospyros walker</i>	x	x
VU	<i>Dipterocarpus alatus</i>	x	x
VU	<i>Shorea guiso</i>		x
EN	<i>Anisoptera costata</i>	x	x
EN	<i>Hopea ferrea</i>	x	

NT near threatened, VU vulnerable, EN endangered, OGF old growth forest, RGF regrowth forest

Rare and threatened species

In Napo there were 9 and 5, while in Dong Na Tard there were 20 and 11 singleton (rare) woody species in the old-growth and regrowth forests, respectively. In general, there were more singleton species found in the old-growth forest than in the regrowth forests. According to the IUCN red list of threatened species both the old-growth and regrowth forests contain threatened species, although the old-growth forests tend to have more (Table 6).

Table 7 Frequency percentage of dominant climber species found in sample plots in Napo and Dong Na Tard

Napo old-growth forest	Napo regrowth forest
<i>Combretum decandrum</i> (50%)	Khuea Song Hang (66.7%) ^a
<i>Dendrobium capillipes</i> (50%)	<i>Aristolochia tagala</i> (50%)
<i>Clinacanthus nutans</i> (50%)	<i>Vitex spp.</i> (50%)
	<i>Tinospora crispa</i> (50%)
	<i>Limacia triandra</i> (50%)
Dong Na Tard old-growth forest	Dong Na Tard regrowth forest
<i>Cleisostoma arietinum</i> (83.3%)	<i>Tiliacora triandra</i> (83.3%)
<i>Toxocarpus villosus</i> (83.3%)	<i>Salacia verrucosa</i> (50%)
<i>Stixis flavescens</i> (66.7%)	<i>Neosomitra sacrophylla</i> (50%)
<i>Gnetum scandens</i> (50%)	<i>Solanum seaforthianum</i> (50%)
<i>Paederia tomentosa</i> (50%)	
<i>Dalbergia rimosa</i> (50%)	
Khuea Khay Khao (50%) ^a	

^aIndicates Lao name**Table 8** The mean herbaceous ground cover percentage in the old-growth and regrowth forests at Napo and Dong Na Tard

Site	Old-growth forest	Regrowth forest
Napo	4.33 (0.89) ^a	0.50 (0.28) ^b
Dong Na Tard	4.17 (0.48) ^a	2.50 (0.62) ^b

Means sharing the same letter (a or b) are not significantly different at $P < 0.05$ (t test). Standard error of the mean is shown in parenthesis

Climber species

Climber species were found abundantly in both the old-growth and regrowth forests; however, the dominant species found in the two forest types were by and large different (Table 7).

Herbaceous species

The old-growth forest had significantly higher herbaceous layer ground cover percentage compared to the regrowth forests (Table 8).

Discussion and conclusions

Old-growth and regrowth forest structure

Compared with regrowth forests, old-growth forests in Napo and Dong Na Tard had higher structural heterogeneity because of higher canopy height variations (uneven canopy), vertical stratification, and tree sizes and their variations. It appears that it takes

Table 9 Reported aboveground biomass (Mg ha^{-1}) values for mixed deciduous forest in Lao PDR and Thailand

Location and forest type	AGB (Mg ha^{-1})	References
Lao PDR	291–364	Brown et al. (1993)
Thailand (mixed deciduous)	266–311	Boonpragob (1998) ^a Ogawa et al. (1965) ^a
Tropical Asia (mixed Forests)	251	(Baccini et al., 2012) ^b

^aCited by Lasco and Pulhin (2004)^bSupplementary data, assuming carbon content is 50% of AGB

considerably longer time (more than 15 years) for regrowth forests in Napo and Dong Na Tard to attain the structure of an old-growth forest. Earlier studies have also demonstrated that it takes several decades for regrowth forests to attain the structure of old-growth forests (Guariguata and Ostertag 2001; Chua et al. 2013; Mukul et al. 2016).

Above-ground biomass (AGB) of the old-growth forests at both sites is similar to other well-stocked mixed deciduous forest in the region (Table 9), but higher than the values reported by Vicharnakorn et al. (2014) for mixed deciduous forest in the Savannakhet Province ($143.95 \text{ Mg ha}^{-1}$), which included heavily degraded forests. This reflects the semi-protected status of the old-growth forest areas in this study, where access rights by the surrounding populations for collecting specific products from the forest might influence forest biomass (signs of recent logging were few in both places, but signs of human activities were clear).

Comparable references for AGB in regrowth forests are difficult to obtain as biomass values are strongly influenced by among other factors, the time the area was under a land use different than forest, the activity in place before abandonment, any soil treatment, and whether remnant trees were maintained during the non-forest phase. Regrowth forests of similar ages from Myanmar report average biomass values close to the ones reported in this study (Table 10). However, these values are well below other less disturbed regrowth forests ranging from 148 to 224 Mg ha^{-1} in the Philippines as reported by Mukul et al. (2016).

Napo's regrowth forest is dense and homogeneous with small diameters and few trees reaching above the closed canopy and these characteristics suggest an even aged forest sharing the same genesis. Dong Na Tard's regrowth forest was structurally less homogeneous and remnant trees were easily spotted. The remnant trees in the canopy were dominated by *Xylopia vielana*, *Cratoxylum formosum*, and *Anisoptera costata*, which were all used locally; *Xylopia* and *Cratoxylum* are both medicinal plants while *Anisoptera* is an endangered valuable timber tree.

Table 10 Reported aboveground biomass (Mg ha^{-1}) values for regrowth mixed deciduous forest in Lao PDR and Myanmar

Location and age/forest type	AGB (Mg ha^{-1})	References
Myanmar (10 years)	17	Chan et al. (2013)
Myanmar (15 years)	38	Chan et al. (2013)
Laos (disturbed forest)	28	Vicharnakorn et al. (2014)

The size class structure of regrowth forests differs from that of old-growth forests, such that it is more skewed towards the younger trees (Fig. 4). The high number of seedlings and saplings in the regrowth forests show that there was a robust natural regeneration, which in turn indicates that there was adequate supply of seeds via seed rain and/or the soil seed bank contained sufficient amount of viable seeds, which may be the pre-disturbance legacy of the site. In addition to germination from seeds, resprouting may have also contributed substantially to the natural regeneration, particularly if the site was cultivated for a short period.

Floristic diversity and composition

In general, the regrowth forests tend to have similar species richness (except in Dong Na Tard), diversity indices and evenness values compared to the old-growth forests (Tables 2, 3). The findings of this study are in agreement with earlier studies which state that species richness of tropical regrowth forests can increase very fast and reach that of old-growth forest in a few decades (Guariguata and Ostertag 2001; van Breugel 2007; McNamara et al. 2012). The proximity of the regrowth forests to the old-growth forests (literally bordering each other) may be the main reason for the fast recovery of species richness in the regrowth forests. It was demonstrated in this study that in general species richness recovers more rapidly than forest structure and this is in line with earlier findings (Piotto et al. 2009; Mukul and Herbohn 2016).

On the other hand, the woody species abundance of regrowth forests was considerably higher than that of old-growth forests. For instance, the woody species abundance of regrowth forests in Napo was almost twice that of the old-growth forest. The finding of this study is in accordance with other studies which state that stem density in regrowth forests is generally higher than old-growth forests (Chazdon et al. 2007).

Although by and large similar in species richness, the regrowth forests were significantly different from the old-growth forests in terms of species composition as shown by Fig. 5a, b and Table 4. This difference in species composition is also illustrated by Table 5a, b, i.e. the indicator species for old-growth forests in Napo and Dong Na Tard were entirely different than that of the regrowth forests. It seems regrowth forests were dominated by some widespread species as indicated by the relatively lower standard deviation of the Bray–Curtis similarity index and lower range of similarity values (Fig. 6). This finding concurs with earlier studies which state that regrowth forests are dominated by early successional and widespread habitat generalist species (Cain and Shelton 2001; Peña-Claros 2003; van Breugel 2007; Edwards et al. 2017).

In the later phase, because of the persistence of long-lived pioneer species and the long turnover time of canopy trees, species composition of regrowth forests takes considerably longer time to approach that of old-growth forests compared with forest structure and species richness (Guariguata and Ostertag 2001; van Breugel 2007; Dent and Wright 2009; Chua et al. 2013). In general, it appears that regrowth forest woody species richness recovers first followed by forest structure and species composition. By and large, regrowth forest recovery in terms of structure, species richness, and composition depends on land-use history, distance to an old-growth forest, ongoing disturbance, etc. (Sovu et al. 2009; McNamara et al. 2012).

Notwithstanding, regrowth forests being useful in conservation of woody species, they do not, however, harbour the full suite of species found in old-growth-forests, particularly the dispersal limited late-successional species. Furthermore, old-growth forests

tend to contain relatively more rare species as found in this and previous studies (Brunialti et al. 2010; Ngo and Hölscher 2014; Shima et al. 2018). The structural heterogeneity of old-growth forests, which is manifested by high tree height and diameter class variations and higher number of strata, provides niches for various species (McElhinny et al. 2005; Gao et al. 2014). Hence, the conservation of old-growth-forests nearby regrowth forests, which serve as source of propagules and a habitat for numerous species are crucial for the conservation of the woody species diversity within a landscape (Dent and Wright 2009; Gibson et al. 2011).

Woody climbers (lianas) and vines were quite abundant in the old-growth and regrowth forests at Napo and Dong Na Tard. This observation concurs with earlier findings which state that woody climbers are common and they are one of the main growth forms in tropical forests—they constitute ca. 25% of the woody stem density (abundance) and species diversity (Schnitzer and Bongers 2002). The most frequent and dominant woody climber species found in old-growth forests were by and large different than the ones found in the regrowth forests (Table 7). In other words, the woody climbers found in the regrowth and old-growth forests may represent the early-successional and late-successional species, respectively.

The herbaceous ground cover percentage of the old growth-forests were found to be significantly higher than that of the regrowth forests at both sites. This is most probably due to the low amount of light reaching the forest floor as a result of the high stem density and relatively uniform canopy (in terms of height) of the regrowth forests.

Implications for conservation and rehabilitation

Regrowth forests are continuing to proliferate throughout the tropics. It is reported that as much as 60% of the world's remaining tropical forests are degraded and regrowth forests (Dent and Wright 2009). Hence, in addition to the declining pristine forests, regrowth forests are of paramount importance in conservation and restoration of tropical biodiversity and they can also serve as a conduit for the restoration of degraded lands and forests.

This study showed that after about 10 to 15 years, regrowth forests can have a similar species richness as that of an old-growth forest and they have a potential to serve as biodiversity repositories. One of the main factors affecting the recovery of regrowth forests is the proximity to old-growth forests and hence the protection of particularly older regrowth forests, which are close to old-growth forests should be given a priority. In addition, regrowth forests of different age groups may have species assemblages belonging to different successional groups and need to be protected (Chazdon et al. 2009). In general, as Crouzeilles et al. (2016) suggest, areas with an intermediate degree of disturbance such as regrowth forests, should be considered a priority for landscape restoration activities as they have the potential for larger gains associated to biodiversity and vegetation structure, thus increasing the conservation value of any given investment. However, at present regrowth forests are underrated and the deforestation of regrowth forests is about three times higher than other forest categories in the lower Mekong Basin (Heinimann et al. 2017).

As there is significant difference in species composition between regrowth and old-growth forests, the regrowth forests may not conserve all the species found in old-growth forests. Hence, enrichment planting of rare/threatened and dispersal-limited species with seedlings grown from germplasms that are better adapted to future climate change (Dawson et al. 2011) may be necessary to speed up the recovery process depending on the objectives of the rehabilitation endeavour. On the other hand, regrowth forests are dynamic and

transient in nature and may develop to a forest comparable to an old-growth forest through natural succession, if they are well-connected to an old-growth forest and the past land use was not intensive. In such cases, minimal or no human intervention is required.

Pockets of regrowth forests embedded within a landscape can also serve as a source of propagules for the autochthonous re-colonization of the surrounding degraded or bare forest lands. Degraded lands in the vicinity of regrowth forests can be rehabilitated by converting them to regrowth forests through natural seed dispersal and regeneration, which is relatively inexpensive compared to afforestation or reforestation.

Regrowth forests have also the potential to serve as buffer zones around the fragmented remnant old-growth forests and may ameliorate edge-effects, reduce anthropogenic disturbances, and enhance landscape connectivity (Pardini et al. 2005; Van Breugel et al. 2013). Buffer zones composed of regrowth forests provide additional habitats for the various organisms residing in the core habitat (Chazdon et al. 2009). In addition, regrowth forests can serve as ecological corridors by connecting isolated remnant forest and agroforestry patches, which improves the dispersal and movement of the flora and fauna as well as the viability of small populations in fragmented landscapes (Chazdon et al. 2009; Morse et al. 2009; Schroeder et al. 2010). In particular, regrowth forests located along the riparian zone function as stream bank stabilizer and ecological corridor connecting the up and down stream areas (Heartsill-Scalley and Aide 2003). In general, the strategic location of regrowth forests in the human-modified landscapes is important in terms of in situ biodiversity conservation and rehabilitation of degraded forest lands.

In Laos, about a quarter of the rural population is involved in shifting agriculture and around 34.6% of the forests are affected by shifting cultivation, which is a considerably large forest area (Sovu et al. 2009; Higashi 2015). By protection of the extensive area of regrowth forests, which are established on fallow lands as a result of shifting cultivation, Laos can rehabilitate a substantial part of its degraded forests and increase the forest cover of the country. Laos aims to increase its forest cover to 70% by 2020 (Sovu et al. 2009). This type of mainly passive restoration is a cheap and acceptably quick method. In conclusion, regrowth forests established on fallow lands in Laos can play a key role in biodiversity conservation and restoration of degraded forests and lands; hence, regrowth forests should be given the due considerations in the national forest conservation and restoration policy of Laos.

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